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**Redescription and Reassessment of *Cadlina luarna*
(Ev. Marcus and Er. Marcus, 1967), comb. nov. (Mollusca,
Opisthobranchia, Doridina)**

by

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Inuda luarna is the type species of the problematic genus *Inuda*, and the only species so far assigned to it. Several newly collected specimens from Baja California Sur, Mexico, allowed a redescription of this species. These specimens are clearly conspecific with the original type material of *Inuda luarna*, which was also re-examined, but show some anatomical differences. The external morphology of the living animals of this species, including the presence of mantle glands, is described for the first time.

The anatomical features of *Inuda luarna* are very similar to those of the genus *Cadlina*, and *Inuda* is regarded as a junior synonym of *Cadlina*. *Cadlina luarna* appears to be a basal member of the *Cadlina* clade, and retains several plesiomorphies also present in *Actinocyclus*.

RESUMEN

Inuda luarna es la especie tipo del problemático género *Inuda*, y la única especie que le ha sido asignada hasta este momento. Varios ejemplares recolectados en Baja California Sur, México, han permitido redescubrir esta especie. Estos especímenes son claramente conespecíficos con el material tipo de *Inuda luarna*, que también ha sido re-examinado, pero presentan algunas diferencias anatómicas. La morfología externa de los animales vivos, incluyendo la presencia de glándulas del manto, se describe por primera vez.

Las características anatómicas de *Inuda luarna* son muy similares a las del género *Cadlina*, e *Inuda* es considerado como un sinónimo de este último. Aparentemente *Cadlina luarna* es un miembro basal de *Cadlina*, y mantiene varias características plesiomórficas que también están presentes en *Actinocyclus*.

The genus *Inuda* was originally described by Marcus and Marcus (1967) based on a single species, *Inuda luarna*, which is the type species by original designation. Since then, no additional species have been assigned to the genus *Inuda*, and the systematic position of this taxon remained uncertain.

The anatomy of *Inuda* was studied by Marcus and Marcus (1967), but the information provided was not adequate by modern standards. In addition, the external morphology and coloration of the living animals were unknown.

Most authors agreed to consider *Inuda* as a member of the Chromodorididae (Marcus and Marcus 1967; Skoglund 1991; Angulo Campillo 2000), except for Keen (1971), who placed this genus in its own family-level taxon. However, Rudman (1984), in his review of the genera of Chromodorididae, did not refer to *Inuda*.

This paper redescribes *Inuda luarna* based on newly collected material from Baja California Sur, Mexico, and attempts to determine the relationships of this taxon.

The material examined is deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ), the Museo de Historia Natural de la Universidad Autónoma de Baja California Sur (MHNUABCS) and the National Museum of Natural History, Washington D. C. (USNM).

SPECIES DESCRIPTION

Genus *Cadlina* Bergh, 1879

Acanthochila Mörch, 1869, suppressed by Opinion 812 (ICZN, 1967). Type species: *Doris laevis* Linnaeus, 1767.

Echinochila Mörch, 1869, suppressed by Opinion 812 (ICZN, 1967). Type species: *Doris laevis* Linnaeus, 1767.

Cadlina Bergh, 1878 (*nomen nudum*).

Cadlina Bergh, 1879. Type species: *Doris repanda* Alder and Hancock, 1842 (= *Cadlina laevis* Linnaeus, 1767), by original designation.

Juanella Odhner, 1922. Type species: *Juanella sparsa* Odhner, 1922, by monotypy.

Inuda Ev. Marcus and Er. Marcus, 1967. Type species: *Inuda luarna* Ev. Marcus and Er. Marcus, 1967, by original designation (new synonym).

Cadlina luarna (Ev. Marcus and Er. Marcus, 1967)

Figs. 1–5

Inuda luarna Marcus and Er. Marcus, 1967:182–184, figs 38–44; Keen, 1971:826; Abbott, 1974:356; Farmer, 1980:104; Skoglund, 1991:12; González, 1993:247; Angulo Campillo, 93–94, fig. 41.

TYPE MATERIAL. — LECTOTYPE (here selected): Puerto Peñasco, Sonora, Mexico, 23 mm preserved length, contracted and dissected, leg. P. Pickens (USNM 678405).

REMARKS ON THE TYPE MATERIAL. — There is a single specimen of *Inuda luarna* deposited at USNM. It was collected from Puerto Peñasco, Sonora, Mexico (type locality) by P. Pickens, and has several labels. One of the labels, handwritten by Eveline Marcus, only includes the name of the species. Another label, handwritten by a different person (probably the collector) contains the numbers "14.22." A more modern label, printed with USNM format indicates the name of the species, locality, collector and that this specimen is the holotype of *Inuda luarna*. The two remaining labels (also USNM format) just repeat the taxonomic status and the registration number of the specimen.

Marcus and Marcus (1967) mentioned that they examined two specimens for the description of this species, and did not select either of them to be the holotype. Thus, the specimen deposited at the USNM collection is not the holotype, but one of the two syntypes of *Inuda luarna*. Since the other specimen is untraceable, and its identity could not be confirmed, we designate the available syntype as the lectotype of this species.

ADDITIONAL MATERIAL EXAMINED. — Calerita, Bahía de La Paz, Baja California Sur, Mexico, 23 February 1997, 2 specimens 55–60 mm long, leg. O. Angulo Campillo (MHNUABCS-INV 1808). Calerita, Bahía de La Paz, Baja California Sur, Mexico, 10 April 1999, 3 specimens 20–44 mm preserved length, leg. O. Angulo Campillo (CASIZ 121 103). Ensenada de los Muertos, southeast of La

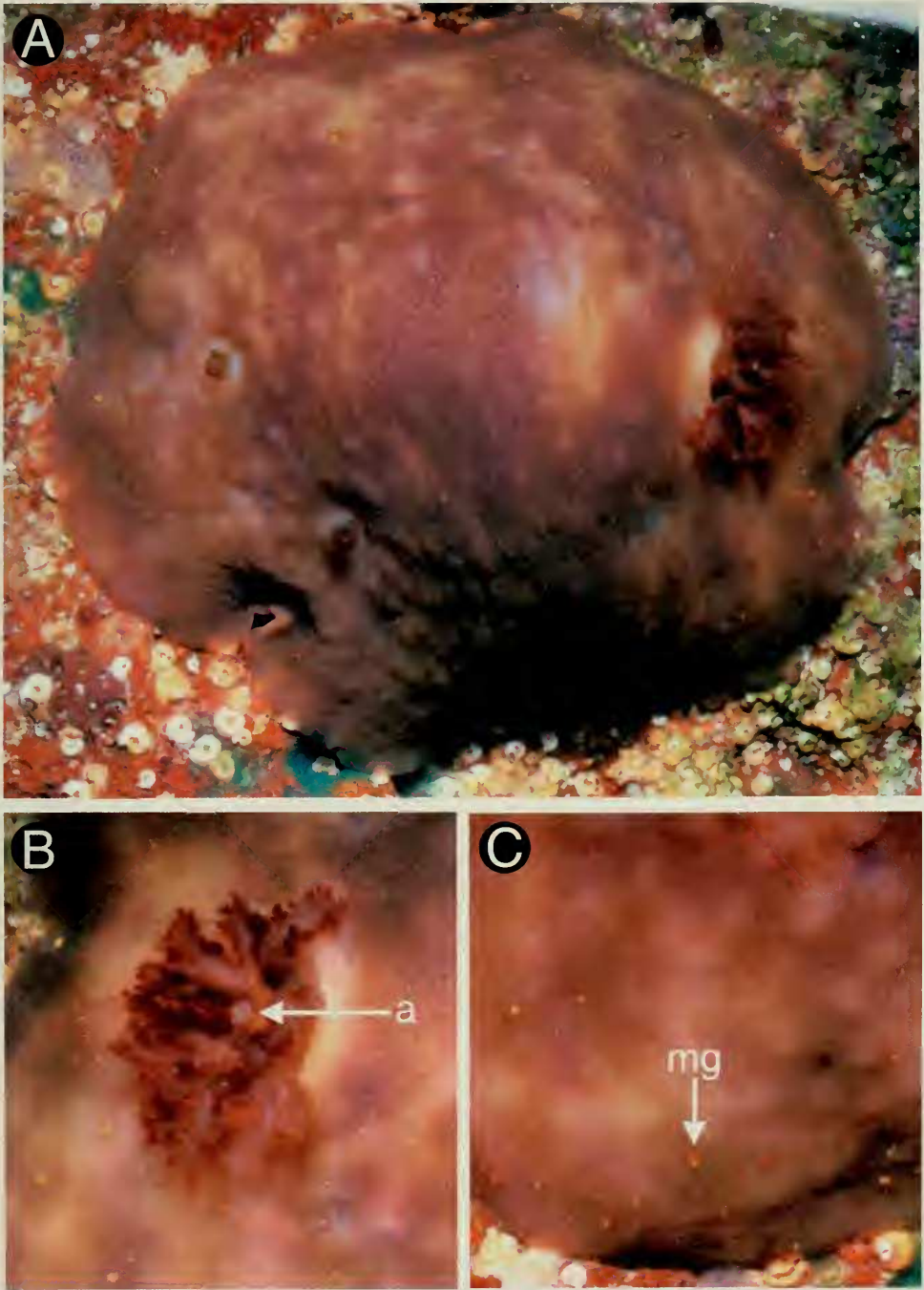


FIGURE 1. Living animal of *Cadlina luarna* from Baja California Sur, Mexico (CASIZ 121104). A. Dorsal view; B. Detail of the gill; C. Detail of the border of the mantle showing mantle glands. Abbreviations: a, anal papillae; mg, mantle gland.

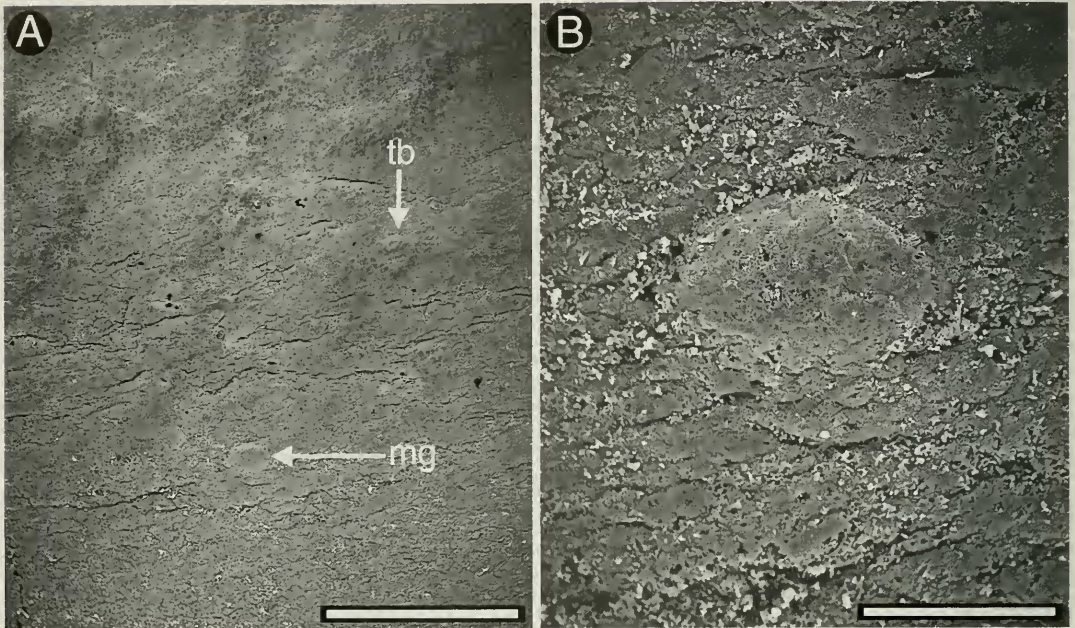


FIGURE 2. Scanning electron micrographs of *Cadlina luarna* (CASIZ 121104). A. Dorsal surface, scale bar = 600 μm . B. Detail of a mantle gland, scale bar = 100 μm . Abbreviations: mg, mantle gland; tb, tubercle.

Paz, Baja California Sur, Mexico, 11 March 2000, 1 specimen 42 mm preserved length, leg. O. Angulo Campillo (CASIZ 121104). Mazatlán, Sinaloa, Mexico, 8 December 1932, 1 specimen 36 mm preserved length, collector unknown (CASIZ 073360).

EXTERNAL MORPHOLOGY. — The body shape is oval to rounded (Fig. 1A). The center of the dorsum is elevated. There are numerous, low and rounded tubercles (Fig. 2A) that are more densely concentrated on the mantle margin. On the mantle margin there are several rows of small mantle glands (Figs 1C, 2B). They are conical in shape and irregularly arranged. The gill is composed of nine bipinnate branchial leaves (Fig. 1B). The perfoliate rhinophores have 12 lamellae. The anal papillae is situated in the center of the circling of branchial leaves (Fig. 1B).

The foot sole is narrow, about half as wide as the mantle margin. The anterior border of the foot is grooved but not notched. The oral tentacles are short and wide, having a deep notch on their ventral side (Fig. 3G).

The background color of the body is pale brown. There are numerous pale creamy white, rounded blotches, that are more densely arranged on the mantle margin. These blotches may be fused together forming larger creamy white areas. The center of the dorsum is covered with minute dark brown spots. The branchial sheath is pale creamy white, and the rhinophoral sheaths translucent gray. The gill and rhinophores are dark brown, with the rachis translucent pale gray. The mantle glands are bright orange.

ANATOMY. — **Digestive system.** The oral tube has three strong muscles that attach to the body wall (Fig. 3D). The muscular buccal bulb is about four times shorter than the oral tube and has two additional muscles attached. The jaws are composed of a number of bifid elements, about 20 μm long (Fig. 4D). The radular formula is $135 \times 65.1.65$ in one specimen examined (CASIZ 121104). The rachidian teeth have a single central cusp, and one or two large denticles on each side (Fig. 4A). The mid-lateral teeth have a strong, short cusp, and one or two triangular denticles on the outer side (Fig. 4B). The outermost teeth are elongate, having one to three small denticles (Fig. 4C). The esophagus

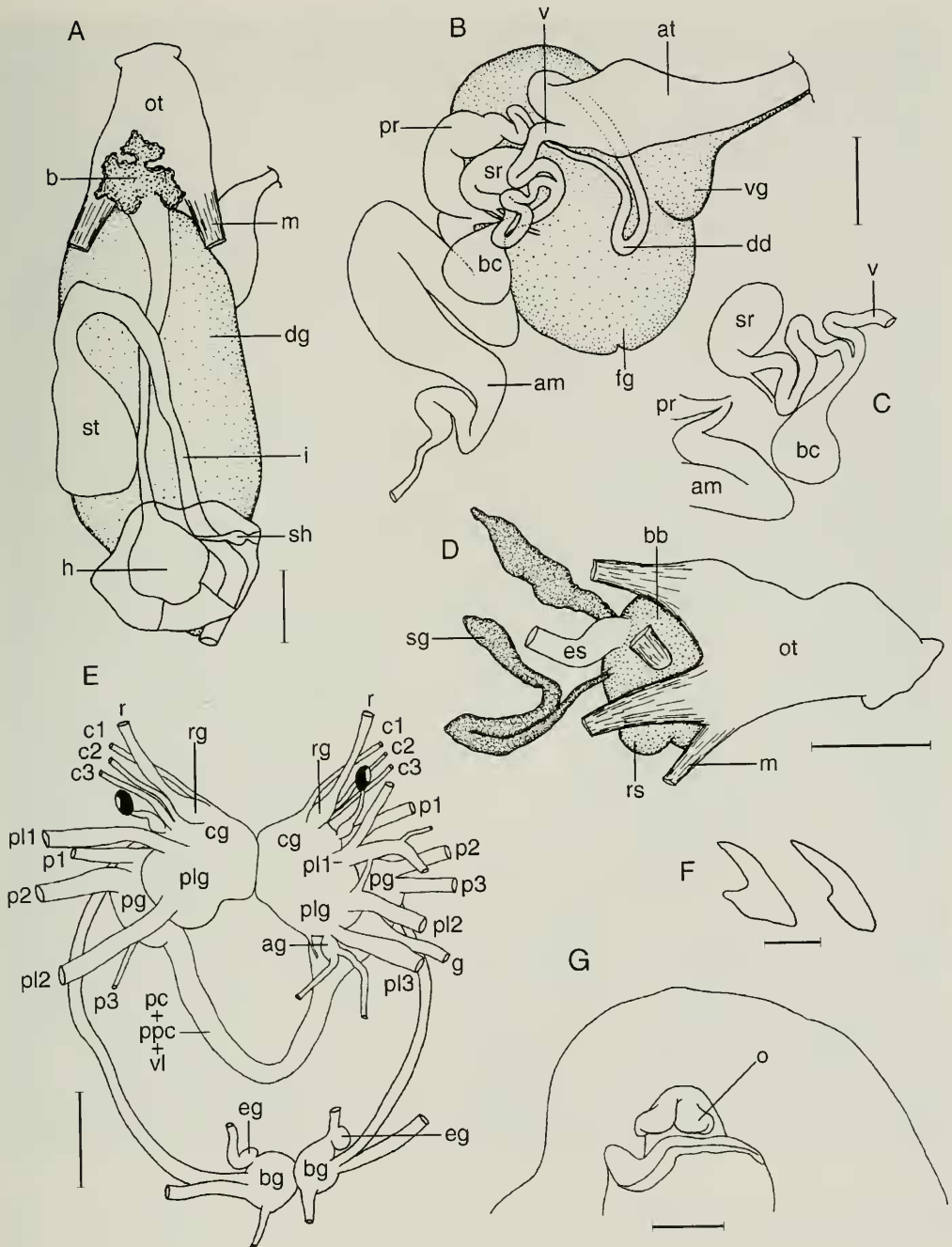


FIGURE 3. Anatomy of *Cadlina luarna*. A. Dorsal view of the internal organs (CASIZ 121104), scale bar = 2 mm; B. Reproductive system (CASIZ 121104), scale bar = 1 mm; C. Detail of several reproductive organs (CASIZ 121104), scale bar = 1 mm; D. Central nervous system (CASIZ 121104), scale bar = 1 mm; E. Lateral view of the anterior portion of the digestive system (CASIZ 121104), scale bar = 1 mm; F. Penial hooks (CASIZ 121104), scale bar = 10 μ m. G. Ventral view of the mouth area (CASIZ 121103), scale bar = 5 mm. Abbreviations: ag, abdominal ganglion; am, ampulla; at, genital atrium; b, blood gland; bb, buccal bulb; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; dd, deferent duct; dg, digestive gland; eg, esophageal ganglion; es, esophagus; fg, female glands; h, heart; i, intestine; m, retractor muscle; o, oral tentacle; ot, oral tube; p, pedal nerve; pc, pedal commissure; ppc, parapedal commissure; pg, pedal ganglion; pl, pleural nerve; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; rg, rhinophoral ganglion; rs, radular sac; sg, salivary gland; sh, syrinx; sr, seminal receptacle; st, stomach; v, vagina; vg, vestibular gland; vl, visceral loop.

opens into the proximal end of the buccal bulb. Near this point two large salivary glands attach to the buccal bulb. The esophagus is short, connecting distally to the digestive gland. The stomach is oval and connects distally to the long intestine, which runs almost straight down to the anal opening (Fig. 3A).

Reproductive system. The ampulla is very long and convoluted (Fig. 3B). It branches into the short oviduct and the prostate. The prostate is short and tubular, but well differentiated. It narrows into the deferent duct, which expands again into the muscular ejaculatory portion. The penis is armed with several rows of hooks (Fig. 3F). These hooks have an elongate cusp about 20 μm long and a shorter base. There is an undifferentiated vestibular gland near the distal aperture of the female glands. The vagina is long and convoluted. At mid-length it branches into a duct that connects to the seminal receptacle and the uterine duct (Fig. 3C). The uterine duct is short and thin, and opens near the center of the female gland mass. The seminal receptacle is slightly oval, almost as large as the pyriform bursa copulatrix.

Central nervous system. The cerebral and pleural ganglia of each side are fused together and are distinct from the pedal ganglia (Fig. 3E). On the right side, there is a distinct abdominal ganglion, connected to the right pleural ganglion. Optical, rhinophoral, buccal, and esophageal ganglia are also present and well differentiated. The pedal and parapedeal commissures are enveloped together by connective tissue with the visceral loop. There are three cerebral nerves leading from each cerebral ganglion and three pedal nerves leading from each pedal ganglion. From the pleural ganglia lead two nerves on the right one and three nerves on the left one.

Circulatory and excretory systems. There is a large heart that connects to a single, ramified blood gland by the aorta. The blood gland is situated covering the central nervous system. The syrinx is small and pyriform.

GEOGRAPHIC RANGE. — This species was previously known from Puerto Peñasco, Sonora, Mexico, which is situated in the north part of the Mar de Cortés (Sea of Cortez). The present paper provides the second record of this species, from the La Paz area, Baja California Sur, and Mazatlán, Sinaloa, and constitutes a range extension of approximately 900 km (Fig. 5). So far this species appears to be endemic to the Gulf of California.

DISCUSSION

Inuda luarna was originally described from Puerto Peñasco, Sonora, Mexico, based on two preserved specimens collected by P. Pickens. The original description of this genus and species (Marcus and Marcus 1967), includes anatomical descriptions and information on the external coloration of the preserved specimens. According to these authors, *Inuda luarna* is a whitish species mottled with brown, due to numerous dots of dark brown pigment. The rhinophores are brown and the gill is darker than the notum. This coloration is very similar to our specimens from Baja California Sur, which are brown with creamy white areas and dark brown spots on the center for the dorsum. In addition, the gill and rhinophores of our specimens are dark brown. Anatomically, the radula described for the Sonora specimens is identical to that of the specimens from Baja California Sur. However, there are some anatomical differences in the reproductive system between the specimens examined by Marcus and Marcus (1967) and our own material. Our specimens have a smaller prostate and a larger ampulla than the animal illustrated by Marcus and Marcus (1967, fig. 43). These differences could be due to a different state of maturity in the specimens studied or to intraspecific variation. Despite these differences, there is no doubt that all the animals belong to the same species.

Marcus and Marcus (1967) considered that the genus *Inuda* resembled *Cadlina* Bergh, 1879, but according to these authors the well-developed prostate of *Inuda* "makes it impossible to allocate these genera in the same subfamily." Thus they erected the new subfamily Inudinae (family Chromodorididae) to accommodate *Inuda luarna*. The subsequent references to this genus and species

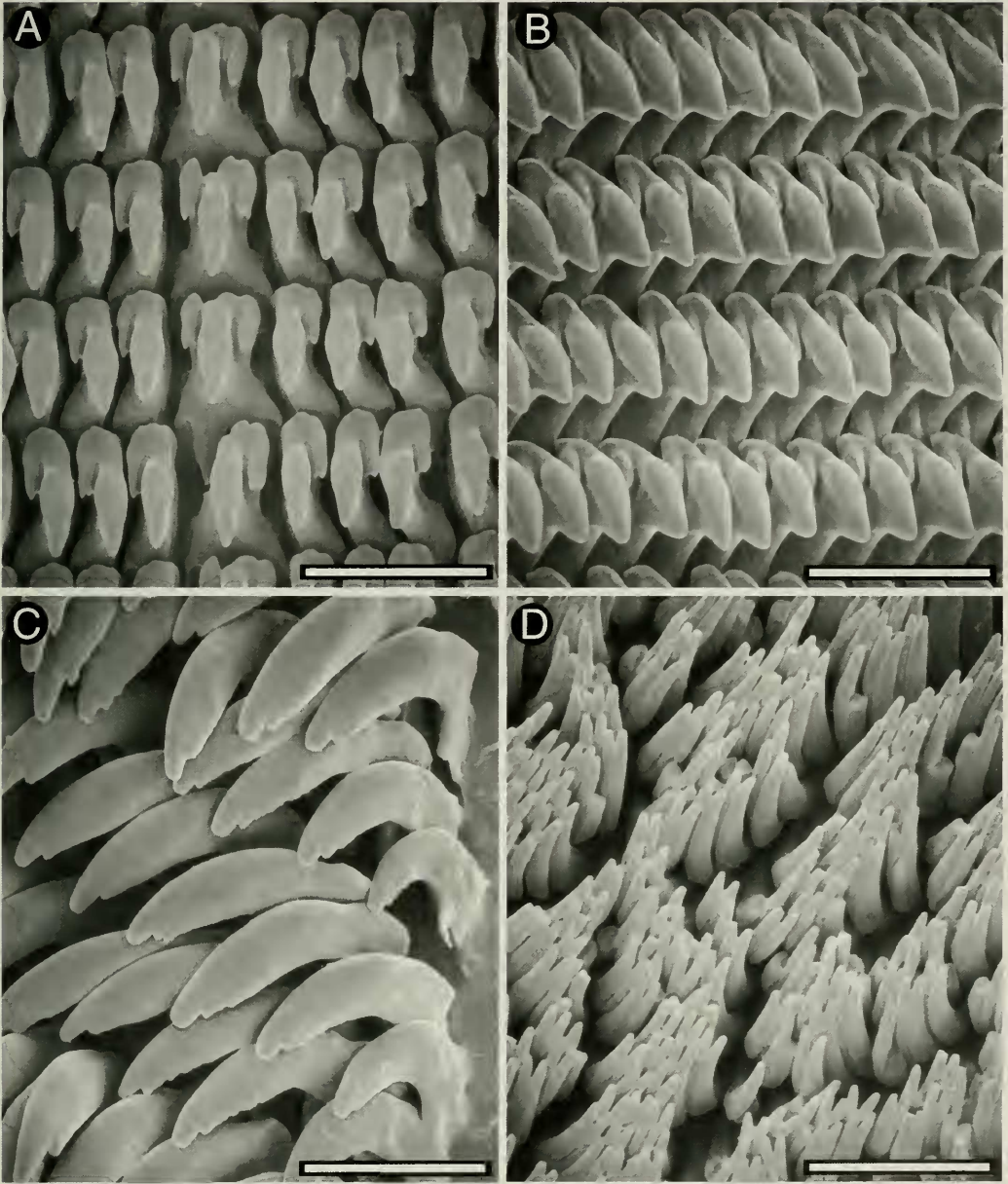


FIGURE 4. Scanning electron micrographs of *Cadlina luarna* (CASIZ 121104). A. Innermost radular teeth, scale bar = 43 μm ; B. Mid-lateral radular teeth, scale bar = 38 μm ; C. Outermost radular teeth, scale bar = 30 μm . D. Jaw elements, scale bar = 23.1 μm .

by Keen (1971), Abbott (1974), Skoglund (1991) and González (1993) are based on the paper by Marcus and Marcus (1967) and not on newly-collected animals. Farmer (1980) re-examined and illustrated the type material of this species but did not provide additional anatomical information. Angulo Campillo (2000) collected additional specimens of this species, which are also re-examined here, and provided the first data on the external coloration of the living animals. All these authors agreed to maintain the genus *Inuda* as valid.

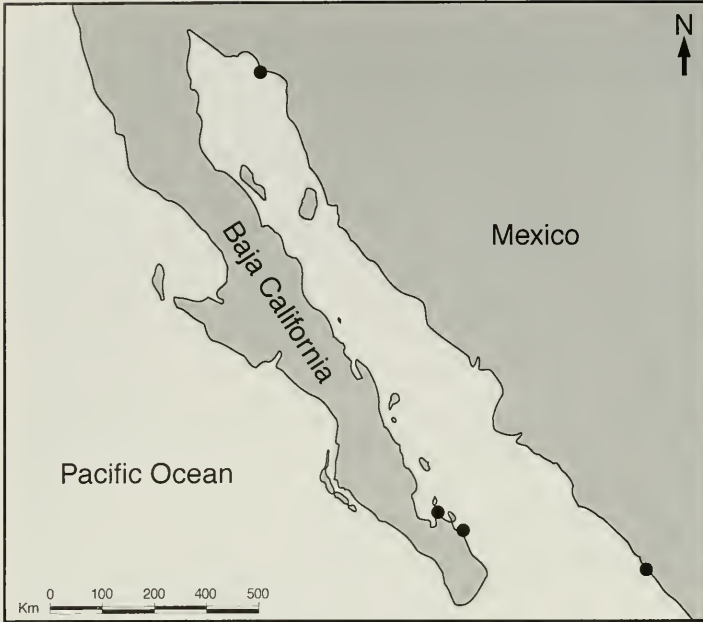


FIGURE 5. Geographic range of *Cadlina luarna* in Mexico.

The presence of mantle glands in *Inuda luarna* clearly places this species in the family Chromodorididae (see Rudman 1984; Gosliner and Johnson 1994; Gosliner and Johnson 1999). These glands were overlooked by Marcus and Marcus (1967), who worked with preserved material. Of all members of Chromodorididae, *Inuda* most resembles *Cadlina*. Rudman (1984) reviewed the genus *Cadlina*, which according to him is characterized by having a heavily spiculate mantle with small tubercles. The mantle glands are large, forming a submarginal row around the mantle. The branchial leaves are simple with a tendency to bipinnate and tripinnate branching. The radula is nar-

row with the number of teeth in the half-row being approximately equal to one-third the number of rows of teeth. The denticles on the teeth are normally few and large. There is a rachidian tooth with no central cusp, but on each side of the midline there are one or two large denticles. Most species have a penis armed with minute hooks. *Inuda luarna* fits this diagnosis, except for the presence of a large, central cusp in the rachidian teeth. In our opinion, this small difference does not justify the maintenance of a different genus, and therefore *Inuda* is here synonymized with *Cadlina*.

Cadlina luarna is clearly different from other species of the genus. The main diagnostic feature is the presence of a well-developed prostate, a character used by Marcus and Marcus (1967) to place this species in a different genus and subfamily. Other species of *Cadlina* present on the west coast of the Americas are *Cadlina flavomaculata* MacFarland, 1905, *Cadlina sparsa* (Odhner, 1921), *Cadlina limbaughorum* Lance, 1962, *Cadlina luteomarginata* MacFarland, 1966, and *Cadlina modesta* MacFarland, 1966. All these species clearly differ from *Cadlina luarna* in having a white or pale creamy white background body color (see Behrens 1991).

Gosliner and Johnson (1994) hypothesized that Actinocyclusidae is the sister clade to the Chromodorididae. Rudman (1984) recognized *Cadlina* to be basal within the Chromodorididae, being the sister group to a clade containing the genera *Glossodoris* Ehrenberg, 1831, *Verconia* Pruvot-Fol, 1931 and *Ardeadoris* Rudman, 1984. Recently Gosliner and Johnson (1999) provided a parsimony-based phylogeny of the Chromodorididae and found *Cadlina* to be the most basal member of a clade containing *Tyrinna* Bergh, 1898 and *Cadlinella* Thiele, 1931, which is the sister group to the rest of the Chromodorididae. The genus *Cadlina* possesses several plesiomorphic features such as spiculate body, rachidian teeth, serial seminal receptacle (Gosliner and Johnson 1999). In addition, *C. luarna* retains plesiomorphies present in *Actinocyclus*, but absent in other members of *Cadlina*. These include a rounded body with an elevated dorsal hump and a well-developed prostate. The arrangement and size of the mantle glands of *C. luarna* also appear to be plesiomorphic. They are smaller than in most members of *Cadlina*, and disorganized, whereas in other species of *Cadlina* they are arranged in a single submarginal row. Another possible plesiomorphy of *C. luarna* is the presence of a large, cen-

tral cusp in the rachidian teeth. According to this particular external morphology and anatomy, *Cadlina luarna* appears to be a very basal member of *Cadlina*, which is also basal within the Chromodorididae. Therefore, this species is extremely important to the study of the phylogenetic relationships within the Chromodorididae and the basal clades of Cryptobranchia.

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